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**Geographic range estimates and environmental requirements for the harpy eagle derived from spatial models of current and past distribution**

**Running title: Geographic range estimates for the harpy eagle**

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## Abstract

Understanding species-environment relationships is key to defining the spatial structure of species distributions and develop effective conservation plans. However, for many species this baseline information does not exist. With reliable presence data, spatial models that predict geographical ranges and identify environmental processes regulating distribution are a cost-effective and rapid method to achieve this. Yet these spatial models are lacking for many rare and threatened species, particularly in tropical regions. The harpy eagle (*Harpia harpyja*) is a Neotropical forest raptor of conservation concern with a continental distribution across lowland tropical forests in Central and South America. Currently the harpy eagle faces threats from habitat loss and persecution and is categorised as Near-Threatened by the International Union for the Conservation of Nature (IUCN). Within a point process modelling (PPM) framework, we use presence-only occurrences with climatic and topographical predictors to estimate current and past distributions and define environmental requirements using Ecological Niche Factor Analysis. The current PPM prediction had high calibration accuracy (Continuous Boyce Index = 0.838) and was robust to null expectations (pROC ratio = 1.407). Three predictors contributed 96 % to the PPM prediction, with Climatic Moisture Index the most important (72.1 %), followed by minimum temperature of the warmest month (15.6 %) and Terrain Roughness Index (8.3 %). Assessing distribution in environmental space confirmed the same predictors explaining distribution, along with precipitation in the wettest month. Our reclassified binary model estimated a current range size 11 % smaller than the current IUCN range polygon. Paleoclimatic projections combined with the current model predicted stable climatic refugia in the central Amazon, Guyana, eastern Colombia, and Panama. We propose a data-driven geographical range to

complement the current IUCN range estimate, and that despite its continental distribution this tropical forest raptor is highly specialized to specific environmental requirements.

**Keywords:** *Harpia harpyja*, harpy eagle, Neotropical raptors, point process models, geographic range size, Species Distribution Models

## Introduction

Defining species distributions in geographical and environmental space is a fundamental component of conservation management (Peterson *et al.* 2011). Yet this information is lacking for many rare and threatened taxa in a rapidly changing environment (Miller 2010; Lawler *et al.* 2011). Assessing geographic distribution and environmental requirements of rare, poorly studied and cryptic species can be problematic due to scarce occurrence data, resulting in limited information for conservation managers to act upon (Pearce & Boyce 2006). For these under-documented species this baseline spatial information is either inadequate, or non-existent, especially in highly biodiverse tropical regions, often where organismal biology is also poorly known (Rodríguez *et al.* 2007; Tobias *et al.* 2013; Wilson *et al.* 2016, Buechley *et al.* 2019). In response to this knowledge gap, spatial modelling techniques have been developed to help direct conservation actions and implement research programs.

Species Distribution Models (SDMs) can overcome deficiencies in information regarding distribution by correlating the underlying environmental data at known occurrences to predict the areas of highest environmental suitability (Scott *et al.*

2002; Elith & Leathwick 2009). On the other hand, ordination approaches define the underlying environmental factors that explain the most suitable environmental conditions for where a given species is found. Combining both SDMs and ordination is an effective method to define the distributional and ecological constraints of a given species (Chase & Leibold 2003; Soberón & Nakamura 2009; Peterson *et al.* 2011). These methods are particularly useful when using species occurrences generated from biodiversity databases when modelling distributions for species in remote, difficult to survey regions (Peterson 2001; Rhoden *et al.* 2017; Sutton & Puschendorf 2018).

The Neotropics are well-known for high avian biodiversity. Yet many birds, including raptors, face multiple threats across the area, largely driven by human activities such as habitat loss, agricultural development and resource over-exploitation (Tobias *et al.* 2013; Sarasola *et al.* 2018, McClure *et al.* 2018, Buechley *et al.* 2019). Due to the difficulties of sampling across the extensive and complex terrain of the Neotropics, applying SDMs using open-access distribution data can generate baseline information on species distributions in a rapid and cost-effective manner (Cayuela *et al.* 2009; La Sorte & Somveille 2020). The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor, with a broad yet shrinking range across Central and South America from southern Mexico to northern Argentina (Ferguson-Lees & Christie 2005; Vargas González *et al.* 2006). Harpy eagles generally occur at low population densities in lowland tropical forest (Vargas González & Vargas 2011) but are nearly extinct in Brazil's Atlantic forest (Srbek-Araujo & Chiarello 2006; Meller & Guadagnin 2016) and in forest enclaves such as riparian forests in open savannahs (Silva *et al.* 2013).

101

102 With generally low population densities and a 3-year long breeding cycle, the harpy  
103 eagle is considered a species of conservation concern due to continued habitat loss  
104 and persecution (Vargas González *et al.* 2006; Miranda *et al.* 2019). Currently  
105 categorised as 'Near-Threatened' by the International Union for the Conservation of  
106 Nature (IUCN; Birdlife International 2017), local extirpations have occurred in most of  
107 Central America, and the population status of the species across its continental  
108 range is largely unknown (Vargas González *et al.* 2006). The current IUCN  
109 geographic range for the harpy eagle estimates an Extent of Occurrence (EOO) of  
110 17.6 million km<sup>2</sup> and an unknown Area of Occupancy (AOO, Birdlife International  
111 2017). EOO measures the area within a minimum convex polygon (MCP) from all  
112 known species occurrences, while AOO is a subset of the EOO where the species  
113 actually occurs in occupied grid cells of 2x2 km, excluding vagrancy (Gaston & Fuller  
114 2009; Brooks *et al.* 2019). Both measures are based solely on spatial locations and  
115 not on underlying environmental information.

116

117 One of the main criticisms of using EOO is that it often includes unsuitable areas,  
118 overestimating the true range, which is more likely to show a discontinuous pattern  
119 of distribution (Jetz *et al.* 2007; Peterson *et al.* 2016; Breiner *et al.* 2017; Ramesh *et*  
120 *al.* 2017). SDMs are useful as an alternative measure to complement IUCN  
121 estimates, intermediate between EOO and AOO, especially for rare and under-  
122 sampled species (Breiner *et al.* 2017). SDMs should not be viewed as surrogates for  
123 IUCN criteria but can provide a basis for estimating AOO (Gaston & Fuller 2009;  
124 Breiner *et al.* 2017; IUCN 2019), especially in the case for the harpy eagle where this  
125 figure is unknown. Using the underlying environmental signature of the species as a

guide for model interpolation may produce a more realistic data-driven estimate of distribution area (Peterson *et al.* 2016). Global range size is a key parameter for assessing threat status and extinction risk, thus overestimating this figure could lead to increasingly threatened species being missed (Ramesh *et al.* 2017). Predicting areas with the highest environmental suitability can thus focus research effort and update threatened species' conservation status (Bierregaard 1998).

Miranda *et al.* (2019) produced the first SDM for the harpy eagle, identifying its close relationship to lowland tropical forest. We build on the strengths of this initial SDM, first by incorporating extra presence-only occurrences with the Miranda *et al.* location data, and second using an expanded set of environmental predictors. Additionally, we project current predictions into two paleoclimatic scenarios and predict how past distributions may influence present and future distribution. Long-term ecological perspectives from paleoclimate models are important for comparing current distribution to past fluctuations (Nogués-Bravo 2009; Fuller *et al.* 2011). Further, having a long-term perspective of past distributions is critical to interpreting current distribution and can point towards potential refugia expected from future changes in range size (Fuller *et al.* 2011; Keppel *et al.* 2012). Understanding the species-environment relationships regulating current and historical harpy eagle distribution can therefore help direct conservation management by identifying the spatial extent for the species.

Here, predictive spatial models are developed for the harpy eagle in geographical space using a point process modelling (PPM) framework. Recently, PPMs have been shown to be most effective for modelling distributions using presence-only

occurrences (Warton & Shepherd 2010; Renner *et al.* 2015). PPMs model the intensity of occurrence points across a given area, thus under low spatial dependence of occurrences the resulting outputs can be interpreted as either the relative (Renner *et al.* 2015), or potential abundance of focal species (Phillips *et al.* 2017). An ecological profile is then developed using ordination with an Ecological Niche Factor Analysis (ENFA) to best explain the environmental requirements of the harpy eagle, compared to the background environmental conditions available. Specifically, we aim to: **(1)** re-evaluate current harpy eagle distribution and establish its ecological niche as a function of climatic and topographical predictors, **(2)** revise the estimated current coarse-scale IUCN distributional area and provide complementary range maps, and **(3)** predict past distributions from two paleoclimatic time periods and combine with the current model to identify stable refugia.

## **Materials and Methods**

### **Harpy Eagle occurrence data**

Harpy eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, The Peregrine Fund 2018) a data information system for all raptor species. For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019), which are mostly eBird records (89.88%, Sullivan *et al.* 2009), combined with two additional datasets of nests and observations (Vargas González & Vargas 2011; Miranda *et al.* 2019). Occurrence data were cleaned by removing duplicate records, those with no geo-referenced location and for spatial auto-correlation (see Appendix 1 in Supporting Information). To account for sampling bias in occurrences, a 4 km spatial filter from each occurrence point was used to minimise the effects of survey bias, using the ‘thin’ function in the R package spThin



(Aiello-Lammens *et al.* 2015). The 4 km thinning distance was selected as a proxy of mean inter-nest distances based on breeding pairs in the Darien region of Panama (Vargas González & Vargas 2011). We used 4 km as a minimum distance knowing that inter-nest distances recorded across the harpy eagle range can vary (Piana 2007; Muñoz-López 2008). After data cleaning, a total of 1179 geo-referenced records were compiled for inclusion in model calibration, generally within the current range defined by the IUCN (Fig. S1, see Appendix 3 in Supporting Information; Birdlife International 2017). Applying the 4 km spatial filter, resulted in 742 occurrence records for use in the calibration models. The resulting occurrence points are thus best reported as locations in continuous space, providing the primary motivation for using the PPM regression framework for subsequent spatial analysis (Renner *et al.* 2015).

## **Environmental predictors**

Thirty-seven bioclimatic and topographical predictors were obtained from the WorldClim (v1.4, Hijmans *et al.* 2005) and ENVIREM (Title & Bemmels 2018) databases. WorldClim variables ( $n = 19$ ) are generated through interpolation of average monthly weather station climate data from 1960-1990. The ENVIREM dataset includes 16 climatic and two topographic variables to complement the WorldClim dataset providing a wider range of potential variables from which to select model predictors. Raster layers were cropped and masked to a delimited polygon consisting of all known range countries (including the states of Formosa, Jujuy, Misiones and Salta in northern Argentina, and the states of Chiapas, Oaxaca, and Tabasco in southern Mexico), to extend into potential areas of marginal habitat on the distribution edges. Reducing the accessible area to the known range improves

model predictive power by reducing the background area used for testing points used in model evaluation (Barve *et al.* 2011; Radosavljevic & Anderson 2014).

For past predictions, three General Circulation Models (GCMs, Table 1) were used from the Coupled Model Inter-comparison Project Phase 5 (CMIP5) and Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases for two paleoclimate scenarios in the Mid-Holocene (~6,000 cal yr BP) and Last Glacial Maximum (~22,000 cal yr BP). Three GCMs were used to account for variation and uncertainty in model predictions (Nogués-Bravo 2009), and a summed prediction calculated from all models for both paleoclimate scenarios. Each summed paleo-distribution was then stacked with the current distribution and overlaid to provide a summed estimate of environmental stability (Peterson *et al.* 2017), using the 'stability' function in the R package 'sdStaf' (Atauchi 2018). Summed stability can predict areas of stable refugia, where a species is predicted to be present irrespective of time period (Carnaval *et al.* 2009). Geographic niche overlap from the individual GCMs was tested using Schoener's *D* (Schoener 1968, Warren *et al.* 2008), which ranges between 0 (no overlap) to 1 (identical overlap). Paleoclimate raster data were downloaded from the WorldClim (v1.4, Hijmans *et al.* 2005) and ENVIREM (Title & Bemmels 2018) databases and masked to the current range extent to predict areas of past climatic suitability compared to the current range.

Multicollinearity between environmental predictor variables can bias models by over-representing the biological relevance of correlated variables (Franklin 2009; Phillips *et al.* 2006). Before model construction, environmental cells containing occurrence records from all 37 variables were tested for multicollinearity using Variance Inflation

226 Factor (VIF) analysis (Guisan *et al.* 2006; Hair *et al.* 2006) with the ‘corSelect’  
227 function in the R package fuzzySim (Barbosa 2015, 2018). A stepwise elimination of  
228 highly correlated variables was used retaining predictors with a VIF threshold < 10  
229 considered as suitable for multi-variable correlation (Dormann *et al.* 2013). The  
230 remaining variables were then checked for collinearity using Spearman’s Correlation  
231 Coefficient with only variables  $r_s \leq |0.7|$  retained for consideration as predictors. We  
232 used solely climatic and topographical predictors as to our knowledge there are no  
233 reliable estimates of landcover extent or anthropogenic impact extending back to the  
234 two paleoclimate scenarios used here.

235

236 After removing highly correlated variables, eight climatic variables (isothermality;  
237 maximum temperature warmest month; precipitation wettest month; precipitation  
238 warmest quarter; Climatic Moisture Index (CMI); minimum temperature warmest  
239 month, potential evapotranspiration (PET) driest quarter; PET wettest quarter), and  
240 one topographic variable, Terrain Roughness Index (TRI), were included as  
241 predictors at a spatial resolution of 2.5 arc-minutes (~4.5km resolution). Final  
242 predictor selection was based on representing monthly and seasonal climatic trends,  
243 extremes and limiting environmental factors strongly related theoretically and  
244 empirically to species distributions (Stockwell 2006; Bradie & Leung 2017; Guevara  
245 *et al.* 2018; see Appendix 1 in Supporting Information). For example, in tropical  
246 forests rainfall regime and seasonality are predicted to have a strong effect on avian  
247 survival, food availability, and reproductive effort (Stotz *et al.* 1996; Williams &  
248 Middleton 2008). Therefore, predictors were selected based on seasonal and  
249 monthly precipitation interacting with temperature, as potential limiting factors on  
250 harpy eagle distribution (Williams & Middleton 2008; Busch *et al.* 2011).

251

## 252 **Species Distribution Models**

253 SDMs were fitted using a point process modelling (PPM) framework as a form of  
254 infinitely-weighted logistic regression via penalized maximum likelihood (Fithian &  
255 Hastie 2013), treating occurrences as points rather than grid cells in the R package  
256 maxnet (Phillips *et al.* 2017) and maximum entropy software, MAXENT (v3.4.1).  
257 Recent theoretical work has demonstrated the equivalence of MAXENT to an  
258 inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton  
259 2013; Renner *et al.* 2015), which is the most appropriate method for fitting presence-  
260 only SDMs (Warton & Shepherd 2010). The complementary log-log (cloglog)  
261 transform was selected as a continuous index of environmental suitability, with 0 =  
262 low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog  
263 transform is equivalent to an IPP and can be interpreted as a measure of relative  
264 occurrence probability proportional to a species relative abundance.

265

266 We randomly selected 10,000 background absences recommended for regression-  
267 based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the  
268 background calibration environment (Guevara *et al.* 2018). Convergent threshold  
269 was set at  $10^{-5}$  and iterations increased to 5000 from the default (500) allowing for  
270 model convergence. Optimal-model selection was based on Akaike's Information  
271 Criterion (Akaike 1974) corrected for small sample sizes (AIC<sub>c</sub>; Hurvich & Tsai 1989),  
272 to determine the most parsimonious model by tuning two key MAXENT parameters:  
273 regularization multiplier and feature classes (Warren & Seifert 2011). Eighteen  
274 candidate models of varying complexity were built by comparing a range of  
275 regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes

(Linear and Quadratic) in all possible combinations using the 'checkerboard2' method of cross-validation ( $k$ -folds = 5) within the ENMeval package in R (Muscarella *et al.* 2014). Response curves, parameter estimates, percent contribution, permutation importance and a jack-knife test were used to measure variable performance within the best-fit model (see Appendix 1 in Supporting Information).

## **Model evaluation**

Optimal model selection was evaluated using Area Under the Curve (AUC), and omission rates. AUC is a non-parametric, threshold-independent measure with AUC = 1.0 indicating maximum predictive performance, and AUC = 0.5 being no better than a random prediction.  $AUC_{DIFF}$  ( $AUC_{TRAIN} - AUC_{TEST}$ ) was used to quantify model over-fitting (Muscarella *et al.* 2014), with a value close to zero indicating a low over-fit model (Warren & Seifert 2011). AUC metrics were used as a measure of optimal model selection, best suited to comparing a range of candidate models (Lobo *et al.* 2008; Jiménez-Valverde 2012). Omission rates are threshold-dependent metrics for evaluating discriminatory ability and over-fitting at specified thresholds. Lower omission rates show improved discrimination between suitable and unsuitable areas (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson 2014). Omission rates were calculated based on two threshold rules: minimum training presence (MTP) and 10% training presence (10TP). For low over-fit models the expectation in MTP is a value close to zero and for 10TP a value close to 0.10.

Two further test metrics were used to evaluate the final best-fit model. First, model accuracy was tested against random expectations using partial receiver operating

characteristic (pROC), which estimates model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 – 2 with 1 indicating a random model. Function parameters were set with a 5% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant ( $\alpha = 0.05$ ) pROC ratios  $>1.0$  in the R package ENMGadgets (Barve & Barve, 2013). Second, Continuous Boyce Index (CBI, Hirzel *et al.* 2006) was used to measure how much environmental suitability predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation ( $r_s$ ) with values ranging from -1 to +1. Positive values indicate predictions consistent with observed presences, with values close to zero no different than a random model. Negative values indicate areas with frequent presences having low environmental suitability. Mean CBI evaluation was calculated using five-fold cross-validation on 20% test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

### **Reclassified binary prediction**

To calculate potential range size, the continuous current prediction was reclassified to a binary (suitable/unsuitable) prediction to complement the current IUCN geographic range polygon (BirdLife International 2017). Currently there is no consensus on choosing binary thresholds and threshold selection can be an arbitrary process (Liu *et al.* 2013; 2016). We selected 10% training presence (10TP), a threshold that removes the lowest 10 % of predicted values accounting for any uncertainty in the occurrence data (Pearson *et al.* 2007), and visually best fitted current expert knowledge on harpy eagle distribution. We used the same 10TP threshold for the paleoclimate predictions because this provided a more realistic

estimate for current range size to use for projecting into past climatic scenarios. Finally, we calculated Extent of Occurrence (EOO) with a minimum convex polygon around all our occurrence points (excluding the ocean) following IUCN guidelines (IUCN 2019). General model development and spatial analysis were performed in R (v3.5.1; R Core Team, 2018) using the *dismo* (Hijmans *et al.* 2017), *raster* (Hijmans 2017), *rgdal* (Bivand *et al.* 2019), *rgeos* (Bivand & Rundle 2019) and *sp* (Bivand *et al.* 2013) packages.

### **Environmental ordination**

To determine species-environment relationships in environmental space, the underlying environmental data at occurrence points were extracted using the three most important predictors from their contribution to model prediction. A random sample of 100,000 background points were extracted to represent the background environment, with occurrence data and environmental space defined using a minimum convex polygon. Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002; Basille *et al.* 2008) was calculated using all unfiltered occurrence points ( $n = 1179$ ), against the background environmental data. ENFA directly measures environmental conditions at the presence points, thus spatial auto-correlation in occurrence data is not considered a serious issue (Basille *et al.* 2008). Including as many presence points as possible is therefore advisable in ENFA to obtain accurate measures of occupied environmental space (Hirzel *et al.* 2001).

ENFA is a multivariate, factorial analysis extracting two measures of a species realized niche along two axes. The first axis metric, marginality ( $M$ ), measures the position of the species ecological niche, and its departure relative to the available

environment. A value of  $M > 1$  indicates that the niche deviates more relative to the reference environmental background and has specific environmental preferences compared to the available environment. The second axis metric, specialization ( $S$ ), is an indication of niche breadth size relative to the environmental background, with a value of  $S > 1$  indicating higher niche specialization (narrower niche breadth). A high specialization value indicates a high reliance on the environmental conditions that mainly explain that specific dimension. ENFA was calculated in the R package CENFA (Rinnan 2018), using a corrected calculation on the coefficient matrix for specialization and weighting all cells by the number of observations (Rinnan & Lawler 2019). Predictors were rescaled thus the resulting ENFA can be interpreted similar to a PCA with eigenvalues and loadings represented along the first axis of marginality and the following secondary orthogonal axes of specialization (Basille *et al.* 2008).

## Results

### Species Distribution Models

The best-fit model ( $\Delta AIC_c = 0.0$ ) had feature classes Linear and Quadratic with a regularization multiplier of  $\beta = 1$ . AUC metrics showed moderate predictive performance ( $AUC_{TRAIN} = 0.698$ ,  $AUC_{TEST} = 0.692$ ), with minimal overfitting ( $AUC_{DIFF} = 0.06$ ) and high discrimination ability with omission rates close to expected values (MTP = 0.003, 10TP = 0.11). Testing the model against random expectations resulted in robust mean pROC ratios (pROC = 1.407, SD  $\pm$  0.057, range = 1.235-1.577), with high calibration accuracy between predicted environmental suitability and test occurrence points (Mean CBI = 0.838). The continuous best-fit model defined the spatial complexity in distribution for the harpy eagle, and identified an



area of highest abiotic suitability across Amazonia (Fig. 1), with patchier distribution across southern Brazil and north into Central America (Fig. S3, see Appendix 3). Reclassifying the continuous prediction using the 10TP threshold (0.415; Fig. 2) gave an estimate for geographic range size of 9,844,399 km<sup>2</sup>. Based on our occurrence data we estimated an EOO of 13,050,940 km<sup>2</sup>.

### **Environmental predictors**

From parameter estimates, the harpy eagle was more likely to be associated with CMI and minimum temperature of the warmest month (Table 2). Overall, three predictors contributed 96 % to model prediction. Climatic Moisture Index (CMI) contributed the highest percentage (72.1 %, Table 3), with minimum temperature in the warmest month (15.6 %) and Terrain Roughness Index (TRI, 8.3 %) the next two highest contributions (Table 3). CMI had the highest regularized training gain, followed by precipitation in the wettest month and minimum temperature in the warmest month (Fig. S4, see Appendix 3). CMI had the highest gain when used in isolation, so had the most useful information on suitable environmental conditions when used alone. CMI decreased the gain the most when omitted and could best explain the environmental requirements of the harpy eagle not present in the other predictors.

From the response curves there was a positive response to CMI peaking at ~0.4, with highest suitability for the minimum temperature of the warmest month increasing rapidly after 10°C, peaking at 25°C (Fig. 3). Precipitation in the wettest month peaked at 90 mm/month, before levelling off up to 100 mm, with highest suitability for precipitation in the warmest quarter at 200 mm. Isothermality peaked at 9-10 %,

reflecting the constant temperatures harpy eagles need in lowland tropical forests. PET in the driest quarter had highest suitability at 100 mm/month, but with highest suitability for PET in the wettest quarter at 50 mm/month indicating a preference for climates with greener vegetation. TRI peaked at 100 indicating high preference, as expected, for lowland flat areas with low terrain complexity.

## **Environmental ordination**

Within selected axes of environmental space harpy eagle occurrences were clustered within a Climatic Moisture Index ranging between -0.5 and 0.7 (Fig. 4a). Harpy eagle occurrences showed a lower limit for minimum temperature with no location points below 10.5 °C in the warmest month. Most occurrences were clustered around or above 20 °C (Fig. 4a), linked to the harpy eagle's preference for generally flat, lowland areas with low terrain complexity (Fig. 4b). Harpy eagle environmental space did not deviate substantially from the average background environment available, with the ENFA marginality factor slightly below the available background environment ( $M = 0.99$ ; Fig. 5, red circle). However, the harpy eagle is restricted to a particular environmental space relative to the reference environmental background with a narrow environmental niche breadth indicating highly specialized environmental requirements ( $S = 1.431$ ). Five significant ENFA factors explained 80.75 % of the total variance in niche structure, with the first specialization axis (Spec1) explaining 28.81 % of this total (Table 4). CMI and precipitation in the wettest month were the two highest coefficients on the marginality axis, with minimum temperature in the warmest month the highest on the specialization axis.

## **Paleo-distributions**

All individual paleoclimate GCMs predicted similar paleo-distributions with high geographical niche overlap (Table S1, see Appendix 2 in Supplementary Information; Figs. S5-S6, see Appendix 3). From the mean projections, hindcasting the current prediction to the LGM defined a large area of high suitability across northern-central South America. A further strip of high suitability extended from present-day Panama, south along the Pacific slope west of the Andes into the present-day Chocó region and west Ecuador (Fig. S7, top left). In the Mid-Holocene high suitability areas increased, extending north into Central America, across Amazonia and east in present-day Brazil (Fig. S7, top right). During the LGM mean range size was 17 % smaller (Fig. S7, bottom left; Table S2, see Appendix 2), compared to the current 10TP geographic range size (9,844,399 km<sup>2</sup>). In the Mid-Holocene, range size had increased from the LGM, but was still 6 % smaller than the current 10TP range size estimate (Table S2, see Appendix 2; Fig. S7, bottom right). Areas of highest stable refugia were identified in the central Amazon basin north into Guyana, south-east Colombia and Panama (Fig. 6), consistent with these areas having continuous high suitability since the LGM.

## Discussion

More than half of all global raptor species have declining populations, and there is a significant knowledge gap on the extent of their distribution and ecological requirements (McClure *et al.* 2018). In particular, accurate distribution estimates are lacking for many tropical forest raptors (Sarasola *et al.* 2018; Buechley *et al.* 2019). We provide an analytical framework for applying predictive spatial models to address these fundamental issues to a tropical forest raptor. More broadly, we propose this analytical framework as an efficient and cost-effective approach to tackling this

problem across all taxa. Using a PPM regression framework is now viewed as one of the most effective methods to determine species distributions and relative abundance (Aarts *et al.* 2012; Renner *et al.* 2015; Isaac *et al.* 2019), as supported by our results. Using climatic and topographical predictors resulted in high model predictive performance, defining in more detail the spatial and environmental requirements for the harpy eagle across its geographical range. However, we recognise that including predictors such as landcover and human impact, which are changing rapidly, would improve predictions. These, however, will be analysed and presented elsewhere.

## **Spatial requirements**

How species are distributed in geographical and environmental space is fundamental to conservation planning (Loiselle *et al.* 2003; Pearce & Boyce 2006). Yet accurate and reliable spatial information, such as geographic range size and environmental constraints, are often lacking in many tropical biodiversity assessments (Cayuela *et al.* 2009; Tobias *et al.* 2013), and specifically for Neotropical raptors (Sarasola *et al.* 2018). Using a PPM framework enables the predictions given here to be interpreted as areas of relative abundance (Renner *et al.* 2015; Philips *et al.* 2017) under the assumption that historical habitat is still intact. Building on a previous SDM (Miranda *et al.* 2019), our continuous prediction adds further spatial detail showing a discontinuous distribution. This is likely a consequence of patchy environments, resulting in spatial heterogeneity in harpy eagle distribution. Miranda *et al.* (2019) used both climatic and vegetation predictors, and there is a close visual correspondence between their predictions and both our continuous and binary models. This suggests that at the continental scale biologically relevant climatic and

topographical predictors alone can accurately predict the distribution for the harpy eagle.

Our models refine previous coarse estimates of harpy eagle distribution (Ferguson-Lees & Christie 2005; Birdlife International 2017), providing an empirically-derived range size to complement the species' current IUCN status. Our binary threshold polygon estimate of geographic range size (Fig. 2; 9,844,399 km<sup>2</sup>), was 11 % smaller than the current IUCN polygon (11,064,295 km<sup>2</sup>), and our estimated EOO (13,050,940 km<sup>2</sup>) was 25.9 % less than the current IUCN EOO (17,600,000 km<sup>2</sup>). Based on these figures we recommend reviewing the IUCN distributional area for the harpy eagle, which can over-estimate avian geographic range sizes (Jetz *et al.* 2008; Peterson *et al.* 2016; Ramesh *et al.* 2017). Specifically, the removal of semi-arid areas (such as the Caatinga in eastern Brazil) from across the IUCN range would show a more realistic geographic distribution. The Caatinga area had low predicted suitability, no current or historical occurrence records, and was not predicted suitable for the harpy eagle including during the last glacial maximum (LGM). Similarly, the Cerrado (in central Brazil) was not predicted as suitable for the harpy eagle either during the LGM, and all recent records for the species show no evidence of breeding in the area. Although early naturalists reported breeding harpy eagles in this region (Sick & Barruel 1984), there is no evidence of a functional population and the area should be removed from the IUCN range polygon (and any present range projections) following IUCN guidelines for not including areas where the species does not exist (IUCN 2019).

## **Species-Environment relationships**

501 The continuous model highlighted distinct areas of high environmental suitability  
502 (Fig. 1), with the binary model closely matching the primary vegetation types for  
503 recognized harpy eagle habitat (lowland tropical broadleaf forest, Beck *et al.* 2018).  
504 Thus, in the Chocó biogeographic region of north-west Ecuador and south-west  
505 Colombia west of the Andes, the current model defined areas of high environmental  
506 suitability, which correlate with new records of harpy eagles in the Pacific slope  
507 region (Muñiz-López 2005; Muñiz-López *et al.* 2007; Zuluaga *et al.* 2018). However,  
508 due to continued habitat loss in this area and across the species range, climatically  
509 suitable areas predicted for some regions may over-represent suitability where there  
510 is no longer harpy eagle forest habitat. Our models also defined previously  
511 unrecognized areas of high environmental suitability in south-east Colombia,  
512 northern Guyana, and along the east Andean slope of Peru and Bolivia. All these  
513 regions may hold viable populations of harpy eagles, with further research and  
514 continued surveys in these areas recommended where possible.

515

516 Environmental suitability predicted for the harpy eagle largely correlates with habitat  
517 selection studies from Amazonian Peru (Robinson 1994). Here, highest frequency of  
518 harpy eagle sightings were recorded in mature flood plain forest, with high nesting  
519 densities below 300 m elevation in lowland humid forest in Darien, Panama (Vargas  
520 González & Vargas 2011), analogous to the environmental suitability predictions  
521 here. Due to the rarity and large home range sizes of harpy eagles, Thiollay (1989)  
522 was not able to provide population density estimates from French Guiana, but  
523 suggested harpy eagles are rare but widespread throughout the largely tropical  
524 lowland forest in the region, consistent with our results. Although largely thought to  
525 be extirpated from much of Central America, our models identify areas of high

suitability for harpy eagles along the Caribbean slopes of Costa Rica, Honduras, Nicaragua and Panama (Fig. S3), which should be prioritised for continued surveys and habitat protection.

Using the combined analytical approach enabled a further development of the spatial modelling process by unravelling the preferred environmental space and ecological conditions where harpy eagle abundance should be at its highest (VanDerWal *et al.* 2009; Osorio-Olvera *et al.* 2019). Climatic Moisture Index (CMI) was the most important environmental variable defining harpy eagle distribution, with a preferred CMI =  $\sim 0.4$  (Fig. 3), along with the highest model gain when used solely in a jack-knife test, demonstrating its importance to account for harpy eagle distribution. This indicates a preference for wet, moist environments, correlating with lowland tropical forest across Central and South America (Willmott & Feddema 1992; Beck *et al.* 2018), and suggests that CMI may be a useful surrogate predictor for habitat in tropical areas. Aligned with CMI and lowland tropical forest distribution was the positive response to higher minimum temperatures in the warmest month (Fig. 3). Harpy eagle environmental suitability was highest in areas with a minimum temperature of  $\sim 24^{\circ}\text{C}$ , reflected in the stable temperature conditions found across lowland tropical forests.

Assessing harpy eagle distribution in environmental space revealed similar patterns of environmental tolerances to the geographical models (Figs. 4 & 5), with CMI having the highest positive correlation with harpy eagle occurrence. However, precipitation in the wettest month was also highly correlated with harpy eagle occurrence (Table 4), following the general observation for tropical regions that

seasonal rainfall patterns are the main limiting factor for primary productivity and therefore species distributions (Schloss *et al.* 1999; Williams & Middleton 2008). The ENFA confirmed the specialized environmental requirements for the harpy eagle, strongly linked to CMI and precipitation, which are likely operating as useful surrogate predictors of lowland tropical forest habitat. Importantly, minimum temperature of the warmest month (MTWM) had a high negative coefficient value on the specialization axis (Table 4). This indicates that MTWM is a key climatic predictor restricting harpy eagle distribution, linked to harpy eagle preference for lower elevations (Piana 2007; Muñiz-López 2008; Vargas González & Vargas 2011). Harpy eagle nests are rarely found above an altitude of 300m (Vargas González & Vargas 2011), and as temperature and elevation are closely correlated it seems likely the harpy eagle is negatively responding to lower temperatures at higher elevations restricting breeding distribution.

### **Paleo-distributions**

The two paleoclimate predictions given here place current harpy eagle distribution in context. During the LGM, highest suitability was centred on northern and western Amazonia and present-day Panama. This follows current evidence that suggests during the LGM much of Amazonia was forested (Mayle *et al.* 2004), contrary to the rainforest refugia hypothesis (Haffer 1969). However, forest structure was likely quite different from the present-day, due to lower temperatures, rainfall and atmospheric CO<sub>2</sub> (Mayle *et al.* 2004), resulting in mixed-forest communities. Climate reconstructions from Amazonia during the LGM show that temperatures were 5°C cooler than today (Guilderson *et al.* 1994; Stute *et al.* 1995), and that rainfall was spatially highly variable, as it is in the present-day. Thus, dry forest-savannahs may



have dominated the region of central and southern Amazonia during the LGM, which may explain the low environmental suitability for the harpy eagle in this region from the LGM paleo-climate model.

During the Mid-Holocene the continuous prediction was similar to the current model with expansion of high suitability across Amazonia and north into Central America (Fig. S7, top right, Appendix 3). This may be explained by the correlation of these areas with expansion of deciduous broadleaf forest in the region during the Mid-Holocene, ultimately related to changing precipitation levels (Mayle *et al.* 2004). The increase in distributional area size during this period correlates with a population expansion identified from genetics from 60,000 cal yr BP, well before the LGM, and subsequently through the Mid-Holocene (Lerner *et al.* 2009). The population expansion prior to the LGM occurred with climatic changes in Amazonia, leading to a reduction of tropical forest (Mayle *et al.* 2004), followed by expansion of forest through the LGM and Mid-Holocene up to pre-Industrial times. Thus, harpy eagle distribution area is strongly associated with changing climatic conditions (and therefore vegetation), which suggests a potential reduction in range size under future drier climate change conditions predicted across much of Central and South America (da Costa *et al.* 2010). However, our stable refugia prediction identified key areas of stable conditions since the LGM where a suitable climatic envelope for the harpy eagle is likely to persist into the future (Fig. 6). We recommend these areas be prioritized for conservation and research, holding some encouragement for the future survival of the species as long as habitat can be maintained.

Explaining the observed distribution and ecological constraints of an organism by reference to its environmental requirements is one of the central goals in ecology (Krebs 2009). Species at high trophic-levels with slow life histories are often at increased risk of extinction (Purvis *et al.* 2000). Therefore, understanding the environmental processes regulating distribution of apex predators is an especially pressing conservation need. By refining previous range estimates using relevant abiotic variables (including those that may act as vegetation surrogates), our models define the ecological processes shaping both current and past harpy eagle distribution. However, future distribution models should include variables such as biotic interactions, landcover and human impacts at broad and fine scales to improve current predictions, and project into future climate change scenarios. With recent work demonstrating strong relationships between suitability predictions from SDMs and species abundance (Weber *et al.* 2017, Osorio-Olvera *et al.* 2020), we confirmed the suitability of spatial point process models to deliver cost-effective and reliable first estimates of relative abundance for species conservation management. Having accurate distributional data on the current ranges of tropical birds and raptors has long been a priority in the Neotropics (Snow 1985; Bierregaard 1998). Using a range of spatial modelling methods, we were able to establish a baseline of ecological constraints for the harpy eagle that may help to better plan its conservation across its vast continental distribution.

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### **Authors' Contributions**

L.J.S., M.F., C.J.W.M., & R.P. conceived the ideas and designed methodology; D.L.A, E.B.P.M., F.H.V. & J.J.V.G collected data; L.J.S. analysed the data; L.J.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### **Conflict of Interest**

The authors have no conflicts of interest to declare.

### **Data Accessibility Statement**

The data that support the findings of this study are openly available on the data repository Dryad: <https://doi.org/10.5061/dryad.9cnp5hqgn>

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## Tables

**Table 1.** General Circulation Models (GCMs) from the Coupled Model Inter-comparison Project Phase 5 (CMIP5) and Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases used to predict past distributions for the harpy eagle to two paleoclimate scenarios in the Mid-Holocene (~6,000 cal yr BP) and Last Glacial Maximum (~22,000 cal yr BP).

GCM	Acronym	Citation
Community Climate System Model, v4	CCSM4	Gent <i>et al.</i> 2011
Model for Interdisciplinary Research on Climate – Earth System Model	MIROC-ESM	Watanabe <i>et al.</i> 2011
Max Planck Institute for Meteorology – Earth System Model - Paleo	MPI-ESM-P	Giorgetta <i>et al.</i> 2013

**Table 2.** Parameter estimates derived from beta-coefficients for the harpy eagle distribution model fitted using Linear and Quadratic feature classes.

Predictor	Linear	Quadratic
Climatic Moisture Index	1.38	-3.62
Minimum temperature warmest month	0.13	*
Maximum temperature warmest month	0.05	*
PET driest quarter	0.03	0.00
Precipitation wettest month	0.02	*
Terrain Roughness Index	0.02	0.00
Precipitation warmest quarter	0.00	*
Isothermality^2	*	-0.01
PET wettest quarter^2	*	0.00

**Table 3.** Percent contribution and permutation importance for variables used as environmental predictors in the current distribution model for the harpy eagle. All values are %.

Predictor	Percent contribution	Permutation importance
Climatic Moisture Index <sup>1</sup>	72.1	43.1
Minimum temperature warmest month	15.6	22.8
Terrain Roughness Index <sup>2</sup>	8.3	12.4
PET driest quarter	3.0	9.8
PET wettest quarter	0.5	5.2
Isothermality <sup>3</sup>	0.2	5.2
Precipitation wettest month	0.2	5.2
Precipitation warmest quarter	0.0	0.7
Maximum temperature warmest month	0.0	0.4

<sup>1</sup> Ratio of annual precipitation to annual evapotranspiration

<sup>2</sup> Variation in local terrain around a central pixel

<sup>3</sup> Mean diurnal temperature range/temperature annual range\*100.

**Table 4.** Variance explained by the five most significant factors (Marg. = marginality; Spec = Specialization) in an Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle environment space. Coefficient values for the nine environmental predictors are ordered according to the highest coefficient values in the marginality factor.

ENFA axis	Marg	Spec1	Spec2	Spec3	Spec4
Variance explained (%)	14.05	28.81	13.82	12.51	11.56
Predictor					
Climatic Moisture Index	0.56	0.24	-0.08	-0.24	0.26
Precipitation wettest month	0.47	0.04	0.00	-0.05	-0.04
Min. temp. warmest month	0.36	-0.72	-0.30	-0.28	-0.27
Isothermality	0.28	0.12	0.03	0.08	0.33
PET wettest quarter	-0.26	-0.35	-0.31	-0.40	0.20
Precipitation warmest quarter	0.25	-0.07	0.01	0.15	-0.15
PET driest quarter	0.23	-0.39	-0.49	-0.19	-0.56
Max. temp. warmest month	0.21	0.31	0.73	0.77	0.57
Terrain Roughness Index	-0.12	-0.17	-0.18	0.23	0.21

## Figure legends

**Figure 1.** Predicted current distribution for the harpy eagle with values closer to 1 having highest environmental suitability. Grey borders represent national borders and internal state boundaries for Argentina, Brazil, and Mexico. Black points define harpy eagle occurrences.

**Figure 2.** Reclassified binary range prediction for the harpy eagle using 10% training presence (10TP = 0.415) threshold. Khaki area is the suitable environmental space above the 10TP threshold, white areas not suitable. Red polygons define current IUCN range for the harpy eagle. Grey borders represent national borders and internal state boundaries for Argentina, Brazil, and Mexico. Blue points define harpy eagle occurrences.

**Figure 3.** Response curves for predictors used in the current distribution model for the harpy eagle.

**Figure 4.** Distribution of harpy eagle occurrences in selected pairs of environmental variables. Grey points are random background environmental points, red points are harpy eagle occurrences. Black hashed line defines the minimum convex polygon of harpy eagle occurrences.

**Figure 5.** Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle environment space (khaki) within the available background environment (grey) shown across the marginality (x) and specialization (y) axes. Arrow length indicates the magnitude with which each variable accounts for the variance on each of the two axes. Red circle indicates niche position (median marginality) relative to the average background environment (the plot origin).

**Figure 6.** Predicted climate stability for the harpy eagle summed from the current, Last Glacial Maximum (LGM, ~22,000 years ago) and Mid-Holocene (~6,000 years ago) predictions. Values of -2 indicate species absence, -1 to 0 shows colonizable areas, 0 to 1 defines areas of highest stability and values of 2 (dark red patches) show the most unstable areas. Map defines summed prediction masked to current geographic extent and geo-political boundaries.